undeservedly fallen, and that it may lead to a stricter supervision of the instruments employed in nautical astronomy. I believe that all gun barrels have to be submitted to a Government test, but if one burst, little harm would be done, except to the user. In the case of sextants and chronometers no supervision is exercised in their manufacture, and the selection is left to individual caprice, yet a faulty one may cause the loss of much property and many lives.

Art. XIV.—*On the Pseudogastrula Stage in the Development of Calcareous Sponges.*

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(With Plate 1a.)

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Thanks to the researches principally of Metschnikoff, Schulze and Barrois, we are now in possession of a tolerably full and accurate account of the development of the Sycon type of calcareous sponges, as represented by the genus *Sycandra*. It is in the hope of contributing a small addition to our knowledge in this department of embryology that the present paper is written.

Before going on to describe my own observations, it will be advisable to give a brief account of the now generally accepted views concerning the history of the development of *Sycandra*—such, for example, as is to be found in Balfour's "Treatise on Comparative Embryology."

The ovum is a naked, amœboid, nucleated mass of protoplasm, which, after fertilization, undergoes the early stages of its development within the tissues of the mother sponge. The ovum first divides vertically into two and then into four segments. The next two divisions are also vertical, and result in the formation of altogether eight pyramidal segments, arranged in a single layer, with a small cavity in the centre, the embryo at this stage being cushion-shaped. Each segment now divides horizontally, so that we have an embryo composed of two layers of eight cells each. Segmentation goes on until the embryo has the form of a hollow sphere—the *Blastosphere*—whose wall is composed of a single layer of cells, eight of which, situate at one pole of the sphere, are distinguished from the remainder by their granular appearance. These eight cells increase to about thirty-two in number, and become pushed in or invaginated, still, however, remaining as a single layer, so as almost to obliterate the cavity of the blastosphere (segmentation cavity). The remaining cells of the blastosphere become much elongated and ciliated. The embryo is still enclosed within the parental tissues. To this stage—characterized by the invagination of the granular cells—the name *Pseudogastrula* has been given; according to Balfour, no importance can be attached to it. The embryo now soon leaves the parent, and by the time this takes place the granular cells have increased in bulk and become completely everted again, still remaining as a single layer.

The free swimming embryo (or larva), known as an *Amphiblastula*, is oval or egg-shaped, and transversely divided into two halves—a front half, composed of a layer of very numerous, elongated, ciliated cells, and a hinder half composed of the layer of granular cells, now thirty-two in number. Some fifteen or sixteen of the granular cells, viz., those which touch the ciliated cells, form a special ring. Balfour states that "during the later periods of the amphiblastula stage a cavity appears in the granular cells dividing them into two layers." This statement appears to be based upon Metschnikoff's observations, to which I shall have to refer presently.

After swimming about for some time, the ciliated half of the larva becomes invaginated into the granular half, obliterating the segmentation cavity and giving rise to the *Gastrula* stage. "The two layers of the gastrula," says Balfour, "may now be spoken of as epiblast and hypoblast." The gastrula next becomes attached to some object by its mouth, the attachment being effected by the granular (epiblast) cells of the special ring already referred to. "Between the epiblast cells and the hypoblast cells which line the gastrula cavity there arises a hyaline structureless layer, which is more closely attached to the epiblast than to the hypoblast, and is probably derived from the former. . . . There would seem according to Metschnikoff's observations to be a number of mesoblast cells interposed between the two primary layers, which he derives from the inner part of the mass of granular cells." *

The principal changes which take place in the development of the fixed larva into the young sponge are the development of spicules in the mesoblast, the perforation of the double wall of the gastrula by the osculum and pores, and the conversion of the hypoblast cells into the collared cells so characteristic of sponges.

Such, then, is the generally accepted history of the development of *Sycandra,* given as briefly as possible. Perhaps the most remarkable feature in its whole course is the *Pseudogastrula.* Although Balfour states that no importance can be attached to this phase of the life-history, it is obvious that a stage of such constant occurrence amongst the Sycons, and found also, according to Keller,† in the Leucons, cannot be entirely meaningless. Sollas, indeed, has made a speculative attempt to explain it on purely theoretical grounds. "We may conjecture," says he, "that the larva which becomes a sponge now, by invagination of the ciliated layer, is a descendent of a form which used to become a coral by the invagination of the other layer, that is, that a form on the way to become a cœlenterate, took the wrong turn for once, and so ended in a cul-de-sac, and became a sponge. Thus the abnormal kind of invagination in Sycandra may be an instance of what is termed 'reversion to an ancestral type;' on the other hand it may simply indicate the balancing play of forces on the young organism, so that it looks as if it could not make up its mind, and was undecided as to whether to turn the flagellated layer inside and become a sponge, or outside, and become a cœlenterate. Between these alternative possibilities, we cannot decide."‡ All this is mere hypothesis, and I venture to hope that the correct explanation of the *Pseudogastrula* stage may be found in the following observations.

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* Balfour, *loc. cit.*

† "Untersuch. über die Anat. und Entw. einiger Spongien des Mittelmeeres." Unfortunately, I am unable at present to obtain access to this work. I cite it upon the authority of Metschnikoff.

‡ "The Structure and Life-History of a Sponge." Proceedings of the Bristol Naturalists' Society., Vol. 3, 1880.

The sponge which formed the subject of my own investigations, is the remarkable form originally named by Carter *Teichonella labyrinthica.* I propose shortly to publish a full account in another place of the anatomy of this sponge ; meanwhile it is necessary to state that it does not belong to the genus *Teichonella* at all, but is a true Sycon—a fact, indeed, which Mr. Carter himself recognises in one of his later papers,* wherein he suggests that its generic name might be changed from *Teichonella* to *Grantia.* The sponge consists of a stalked cup, with a thin and very much folded wall. The flagellated chambers penetrate the walls of the cup in a direction at right angles to the two surfaces and open on the inner surface into the widely expanded cavity, corresponding to the gastral cavity of a typical Sycon ; the osculum being enormously large and bounded by the folded margin of the cup.

I do not wish here to discuss the generic nomenclature of this sponge, which question I reserve for consideration in my forthcoming paper ; but as it certainly cannot be called *Teichonella,* the type species of which I find to be a typical Leucon, I will, provisionally at any rate, adopt Mr. Carter's suggestion and call it *Grantia labyrinthica.*

In a fine specimen of *Grantia labyrinthica,* dredged by Mr. J. Bracebridge Wilson at Easter 1888, whilst I was myself with him, I met with a very large number of embryos. These were found both in the maternal tissues and also lying free in the flagellated chambers. While still within the maternal tissues the embryo lies in a cavity, which is but little larger than itself and lined by a very distinct single layer of flattened endothelial cells (*vide* Fig. 1). This capsule always lies in the thin layer of mesoderm between the wall of a flagellated chamber and the layer of spicules which surrounds it. Hence the capsule is bounded on the outside by the soft and yielding wall of the flagellated chamber, and on the inside by a layer of rigid spicules. As the embryo increases in size the capsule in which it lies becomes correspondingly enlarged, and owing to the manner in which it is bounded this enlargement must take place towards the flagellated chamber. Thus the side of the capsule next to the layer of spicules becomes flattened, while the opposite side bulges out into the flagellated chamber and forms a kind of blister, over which the delicate wall

* "Annals and Magazine of Natural History," July 1886, p. 38.

of the chamber becomes tightly stretched. These relations are of great importance in considering the development of the embryo, and they appear to be perfectly constant. Judging from the figures of Schulze, Barrois, and Metschnikoff, the embryo of *Sycandra* appears to be very similarly situated.

The youngest embryos in *Grantia labyrinthica* are always found near the margin of the sponge-cup, not far from the last formed flagellated chamber. Figure 1 represents the earliest stage found. The embryo here represented may be considered as in a late blastosphere stage, closely resembling the similar stage in *Sycandra raphanus.* The layer of elongated columnar cells is strongly arched, so as to form almost a hemisphere and lift up the wall of the flagellated chamber in the form of a blister as above described (owing to the direction in which the section happened to be taken this is not very well shown in the figure). The ovoid granular cells still form a single layer, or very nearly so, but show signs of proliferation already. This layer is flattened, and it is easy to see from the figure that the flattening is caused by the presence of the layer of rigid spicules beneath them. In this and in all the numerous other embryos which I have examined in the maternal tissues the ovoid granular cells are turned towards the layer of spicules, and the columnar cells towards the flagellated chamber. According to Schulze,* prior to this stage in *Sycandra raphanus* the layer of granular cells is always turned towards the flagellated chamber, but after this stage he finds the embryo in very different positions in the capsule, "gewöhnlich sogar mit dem hellen convexen Zellenlager dem Radialtubus zugewandt," Judging from this change in position, Schulze considers that from now onwards the columnar cells are ciliated. In my sections, made from spirit material, I have naturally enough not observed any cilia.

Even in this early stage of development the segmentation cavity is no longer quite empty, but contains a quantity of very delicate, finely granular, gelatinous-looking tissue (Fig. 1 *mes.*), in which a number of small, deeply staining nuclei are very distinctly visible. This tissue appears to be of constant occurrence, and is probably the commencement of the mesoblast, or mesoderm of the adult. It is quite uncertain from which layer it is derived, but the similarity of the nuclei to those of the columnar cells, and the fact that

* "Zeitschrift für wissensch. Zoologie," Vol. xxv. (Supplement), pp. 271, 272.

some of the latter nuclei—as shown in Figures 1, 2 and 4—are found out of the row, and apparently approaching the segmentation cavity, seems to indicate that it may possibly be derived from the layer of columnar cells. On the other hand, the granular cells, as I have already said, are already showing signs of proliferation, and may possibly have given rise to the tissue in question.

As development goes on the granular cells proliferate rapidly, especially towards the middle of the layer, where they become smaller and more numerous than at the periphery. As they go on increasing they occupy more and more space, and hence, as they cannot project outwards, on account of the rigid layer of spicules beneath them, they become invaginated, and give rise to the *Pseudogastrula* (Figs. 2, 4). The Pseudogastrula, then, is due to a mechanical invagination of the layer of granular cells, caused by their active growth and the peculiar situation of the embryo. These cells do not now, however, form a single layer, as is usually supposed, but a layer several or many cells thick. Such is certainly the case in *Grantia labyrinthica,* and, judging from the observations of Metschnikoff, to which I shall refer more in detail later on, I think it will probably be found to be the case also in *Sycandra raphanus.* The advantage of thin serial sections in the determination of such a point is obvious, and probably this method of investigation will lead to similar results in the case of the latter species.

At about this period of its life history the embryo leaves the maternal tissues, and escapes into a flagellated chamber, by rupture of the outer wall of the capsule (Fig. 3). This rupture of the capsule takes place in a ring, around the base of the blister which the embryo causes on the wall of the flagellated chamber. It involves, of course, not only the wall of the capsule, but also the wall of the flagellated chamber, which by this time has become tightly stretched and the collared cells composing it apparently flattened out. The outer part of the endothelial lining of the capsule and the portion of the wall of the flagellated chamber immediately overlying it appear to come away with the embryo when the latter breaks loose, forming a more or less structureless membrane, closely adherent to the layer of columnar cells (Fig. 4 *s.m.*) After the escape of the embryo the remains of the capsule appear on the wall of the flagellated chamber as a shallow recess lined by flattened endothelial cells (Fig. 3 *e.c.*)

By this time the granular cells have increased so much in bulk, and became so far invaginated as to reduce the segmentation cavity to a mere slit, in which, however, the primitive mesoblastic tissue is still recognisable (Fig. 4.)

The next distinct stage is represented in Fig. 5. The embryo is now solid and almost spherical. The columnar cells have elongated and their inner ends reach nearly to the centre of the embryo. The segmentation cavity is perhaps represented by a dark area in the centre. The granular cells form a hemispherical mass, which is the posterior half of the embryo. This mass has become differentiated into two distinct parts—(1) an external single layer of clearer, more or less cubical, nucleated cells; and (2) an internal mass of highly granular, larger, nucleated cells, which are ovoid or more or less polygonal from mutual pressure.

In the latest stage which I have seen (still within a flagellated chamber), the embryo has become somewhat pointed at the anterior extremity, and the boundaries between the internal granular cells are no longer distinctly visible. Fig. 6 is a diagram of this stage, representing the free swimming embryo as it leaves the parent sponge on its way to seek a place of fixation. As already stated, I have not myself seen the cilia, but there cannot be the slightest doubt, after the observations of so many authors on the living organism, of their existence.

Certain observations of Metschnikoff on *Sycandra* form a strong confirmation of my views as to the development of the Sycon type of calcisponge. This author* states that in the older larvæ, the posterior part, devoid of cilia, does not remain so simple as in the earlier stages. A cavity is developed in it which divides it into two layers. Sometimes also he found and figures (*loc. cit.* Fig. 11) a larva which closely agrees with that represented in my Fig. 5, in which the posterior half consists of an outer layer of epithelial cells and an inner mass of rounded cells closely packed. This internal mass he derives from the inner of the two layers into which the granular cells are first of all divided. Exactly how the original division of the granular cells took place is not made clear. Metschnikoff appears to have observed the fact that there is a division only after the pseudogastrula stage has been passed through. I suspect that the true course of events is very much the same as I have described

* "Zeitschrift für wissensch. Zoologie," Vol. 32, p. 368 *et seq.*

for *Grantia labyrinthica.* Concerning the inner mass of granular cells, Metschnikoff continues, "Diesen Zellenhaufen kann man als Mesoderm deuten, wie es solche Larven beweisen, wo in demselben sich mehrere Nadeln vorfinden (Fig. 13). Ich will nicht behaupten, dass die von mir beschriebenen Stadien durchaus normale sind; ich glaube vielmehr, dass sie uns eine sehr verfrühte Bildung des Mesoderms, resp. der Nadeln repräsentiren, welcher Vorgang aber mit dem normalen qualitativ ganz ähnlich verläuft. Wenigstens habe ich auch an vollkommen regelmässig und normal ausgebildeten Stadien eine, wenn auch bei weitem nicht so stark ausgebildete Mesodermanlage wahrgenommen."

Metschnikoff, then, has certainly seen in *Sycandra* something closely resembling what I have found in *Grantia labyrinthica,* and it is highly probable that the development of the two forms is almost, if not quite, identical. Metschnikoff's interpretation of the appearance of the internal mass of granular cells as an unusually or abnormally early development of the mesoderm is probably due to the fact that in older larvæ he finds this mass to be no longer visible. This fact, however, is easily explained according to my view of the case, which is as follows:—

The embryo already at a very early stage lies within a cavity lined by a special layer of endothelial cells. As it develops it increases greatly in size, and obviously receives nutriment from the mother sponge, probably through the medium of the endothelial cells.* Balfour† has already expressed the opinion that the granular cells of the free swimming embryo are nutritive in function, and this I hold to be correct, though I do not suppose that they take in any food while the embryo is swimming about. I maintain that the granular cells absorb nutriment from the maternal tissues, increase in size, proliferate rapidly, become mechanically invaginated as before explained, and when they have done absorbing nutriment become arranged in a hemispherical mass of large ovoid cells, highly charged with food granules, and an investing epithelial layer (Fig. 5). The embryo is now ready to lead an independent existence, and the internal mass of granular cells is, I believe, a supply of food which enables it to wander for a long distance before becoming

* Compare my account of the embryos of Stelospongos flabelliformis.—*Quart. Jour. Micro. Sci.*, December 1888.

† "Morphology and Systematic Position of the Spongida."—*Quart. Jour. Micro. Sci.*, vol. xix., 1879; also, "Comparative Embryology," vol. i., p. 122.